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BIOLOGY.—*The measure of population divergence and multiplicity of characters.*<sup>1</sup> ISAAC GINSBURG, U. S. Bureau of Fisheries.  
(Communicated by WALDO L. SCHMITT.)

In two previous papers (1937 and 1938) I discussed the problem of the species and its subdivisions and concluded that the lines drawn between these taxonomic categories must of necessity be arbitrary. In the later paper I employed a method for determining the precise divergence between natural populations, based on the character showing the greatest divergence (designated by Davenport, 1898, as the principal character, and the same term used in this paper), for the purpose of drawing pertinent arbitrary lines between those taxonomic categories. The question of multiplicity of characters was mentioned only in a passing manner. This paper takes up this question in some detail.

The determination of divergence may be considered with reference to time and to extent. Each one of these two factors may be considered further with reference to a single character and to a number of characters.

Time is, of course, an important element in divergence. With reference to time, changes that result in the differentiation and isolation of populations from preexisting populations, as manifested by any one character, may be roughly divided into two categories: rapid and slow. The former class may be called explosive evolutionary changes. Changes sometimes designated as mutations are of the explosive kind. (Geneticists have appropriated the use of the word mutation to express the idea of a change in the gene of any kind or degree. I use the word in the original sense, that is, to signify a perceptible change that is sudden, stable, heritable, and of appreciable magnitude, no matter what its immediate cause may be. We need two separate words to express these two ideas.) While probably not infrequent, it is apparently not the usual *modus operandi* of nature in evolution. The biological evidence adduced up to now makes it apparent that evolution, the differentiation of new populations from

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preexisting ones, usually takes place by slow changes. It may be assumed that, in general, each succeeding generation—or at least some individuals thereof—differs, in any one given character, very slightly from the preceding one. The difference between any two successive generations, considered in their entirety as separate populations, is usually so slight as to be imperceptible by our rather crude methods of observation and measurement. But the minute differences are cumulative, and when any two widely separated generations are compared, they may be detected by statistical methods. (It may be possible to test now the truth of this assumption. Possibly some museum has an adequate sample, collected a hundred or so years ago, of a population of plants or animals that reproduce annually and that have a short span of life, say, one or two years. Such a sample, when compared with a sample of the same population as it exists today, would represent an interval of 50 or more generations. With respect to evolution, biologists are usually in the habit of thinking in terms of geological time; but hardly anything is known now in regard to the time factor in evolution. Possibly in some cases an interval of even 50 or 100 generations may produce cumulatively, under natural or wild conditions—leaving out of consideration laboratory or domesticated conditions—a very small but statistically measurable difference. Crampton (1916, pp. 57, 120; 1932, pp. 78, 95) presents evidence to show that some populations of terrestrial gastropods of the genus *Partula* have undergone average morphological changes, sometimes to a considerable extent, during an interval of a little over half a century, as well as changes in their geographic distribution. Although no detailed observations appear to be extant on the span of life, the age at maturity, and the time frequency of reproduction in *Partula*, it seems safe to assume that a year represents the time interval of one generation and quite probably more than one.)

Though time no doubt plays an important role in evolution, it is hardly of practical importance in discussions of the species problem. For one thing it can not now be determined with anything approaching precision, or, more generally, it can not be determined at all. It is also reasonable to assume that there is no sharp line of demarcation between the above two classes of change with respect to time, and that one gradually merges into the other. We recognize only extreme examples of the explosive kind that happen to come under our observation and designate them as mutations. Even in populations undergoing comparatively slow changes there are apparently all degrees of differences in tempo. In general, it is obvious that some

populations, especially those belonging to certain genera, are now in a state of flux, actively changing and proliferating (the taxonomically so-called "difficult" genera are of this kind), while others show no perceptible change during long intervals of time, hardly differing even from their remote, fossil ancestors. Consequently, even if it were possible to use the time factor in determining divergence, we would have to draw arbitrary lines there also, the same as in the determination of the extent of divergence. Furthermore, the time factor, taken by itself, can not be used as a universal criterion in determining divergence. It is obvious that this factor depends on the span of life, age at maturity, fecundity, and length of the reproductive period of the particular population. Primarily it depends on the interval of time occupied by a generation, which, from this standpoint, may be taken to be its actively reproductive period.

Chiefly from a practical standpoint, therefore, the extent of divergence is the important thing to consider. If pairs of closely related, natural populations diverge to approximately the same extent, at least by the principal character, they are to be regarded as of the same taxonomic rank no matter whether they diverged by explosive or by slow evolutionary changes of different degrees.

In determining the extent of divergence the usual existence of a multiplicity of characters introduces a disturbing element. If closely related diverging populations differed by only one character, the extent of their divergence could be expressed readily and almost completely by the measure employed in my paper referred to (1938), or by some similar measure. But diverging populations usually differ in more than one character. The diagram I presented (1937, p. 187), to illustrate the gradual series obtained when the divergences of the chief distinguishing character or the principal character of a number of pairs of populations are arranged in order, may also be used (omitting the horizontal lines) as a general graphic illustration of the divergences of several characters between a single pair of populations. That is, when two closely related diverging populations are carefully studied, we find that usually they differ in several characters showing different degrees of divergence. The difficulty introduced by the usual existence of several diverging characters as between any given pair of populations was obviated by me (1938) by using the principal character as the basis of determining and measuring the extent of divergence. This method is seemingly incomplete. How are we to express the degree of divergence of two closely related populations by taking into consideration other characters in which they diverge



in addition to the principal character? What weight, if any, are these other characters to be given in measuring divergence? An altogether satisfactory answer to this question can not be given at present; but apparently not much weight should be placed on the other characters.

The problem of the measure of divergence as related to a multiplicity of characters may also be considered with reference to time and extent. With respect to time it is reasonable to assume that when a pair of populations diverge in more than one character, the several characters, in general, change about simultaneously, although this is probably not always and not altogether so. Consequently, it seems probable that the time element is usually of not much importance in determining the hypothetical sum total of divergence of all the characters. As far as the time factor is concerned, the principal character apparently forms an adequate basis for a measure of divergence. In any case, the time factor is not definitely determinable, and we are forced to leave it out of consideration in practice. While the time factor is of much theoretical interest, its consideration at present must be almost altogether of a speculative nature. For practical work in taxonomy we must rely on the extent of divergence. This is the factor of much practical importance in taxonomy, and it may be determined with some measure of precision.

(Geneticists may be dissatisfied with some of the above statements. For instance, some would probably object to the idea of changes being cumulative in an accretive sense, with reference to degrees of magnitude in the development of a given character; and would restrict the idea to a statistical sense, that is, the gradually cumulative addition to the population of individuals showing a given change or changes. With respect to any one presumably single factor character, they probably would express the idea of a cumulative change in a population in their language, in terms of a change, for some largely unknown causes, in the frequency ratios of alternative alleles. With respect to several characters, or any one presumably multiple factor character, they may want to express the idea as the statistical accumulation of mutant genes in the population. However, I am speaking here from the point of view of the taxonomist. The chief cause of difference in the points of view of taxonomists and geneticists is that the latter deal mainly with a particular and comparatively restricted kind of differences, qualitative differences; whereas taxonomists deal with all kinds of populations, and the great majority of closely related populations differ quantitatively, not in the absolute, but in having different frequency distributions that very often overlap, even in those populations that are generally regarded by taxonomists as of the rank of species. Because of the difference, by and large, in the material with which they work, they even think in different terms. Geneticists usually think of characters as of something being present or absent, or as of something that may manifest one form of two or more alternative and more or less discrete forms. Taxonomists, on the other hand, in consequence of the things with which they are more

familiar, generally think of characters as being variables that vary in a gradual manner about a more or less central mode, and in case of continuous variables, in virtually infinitesimal gradations. Another consequence is that in considering divergence between closely related populations, geneticists appear to think of and often lay stress on its being discrete or discontinuous, whereas taxonomists think in terms of degrees of magnitude that are virtually infinitesimally graded.

If current ideas regarding multiple factors and manifold effects of single genes are accepted as a working hypothesis, the proposition of a cumulative change in degrees of magnitude of a gradually variable quantitative character is not excluded, on the assumption that the change in the visible character is due to changes in a number of genes. Therefore, no matter how the propositions are stated, they refer to the same conclusion, that is, the usual way in which perceptible evolutionary changes in populations are brought about in nature is by the slow accumulation of minute differences.

The business of the taxonomist is to distinguish populations—species, subspecies, and races—by their visible morphological characters. The determination of their genetic constitution is a coordinate but, in practice, a separate problem. While a good beginning has been made toward an understanding of the operation of the genetic factors in heredity, it is only a beginning, and it may be expected that current hypotheses will be modified with increased knowledge. What the taxonomist is doing is to study the end products of the very complex interaction of genetic factors. A proper synthesis of the two closely allied branches of biology, genetics and taxonomy, is sorely needed. Perhaps, in the present state of knowledge, the time is not yet ripe for such a constructive synthesis. Meanwhile, I am here speaking the language of the taxonomist. The statements made above flow as a plausible consequence of his experience. They also do not seem to be in conflict with the known facts so far uncovered in genetic studies.)

The *extent* of divergence of a multiplicity of diverging characters may be considered by referring to some hypothetical populations. Let us assume a pair of closely related populations, *alpha* and *beta*, that differ by two characters, *A* (Fig. 1) and *B* (Fig. 2). The divergence of character *A* is such that no intergrades exist; that is, the extent of divergence is 100 percent, every individual may be definitely referred to one or the other population on the basis of this character; while character *B* shows a very high degree of intergradation. Let us assume further another pair of population, *gamma* and *delta*, that also differ by two characters, *C* (Fig. 3) and *D* (Fig. 4), both characters showing a moderate degree of intergradation. Character *D*, as indicated in the figure, is assumed to show a slightly higher degree of intergradation than *C*, and *C* is, therefore, the principal character as between these two hypothetical populations. In this hypothetical case a number of individuals are not definitely referable to either population on the basis of any one character. When both characters are considered a number of such intergrades will likely be placed with a satisfactory measure of assurance by one of the characters falling

near the mode or even near the outer extreme end of the distribution of its population; but a residue of the individuals will likely have both characters intergrading.

Judged by criteria now in practical use by biologists in distinguishing populations, it is evident that the first pair of the foregoing two hypothetical pairs of populations shows a relatively greater extent of divergence than the second pair, because every individual, without exception, can be definitely referred to its proper population. The relative degree of divergence between the first pair of populations,

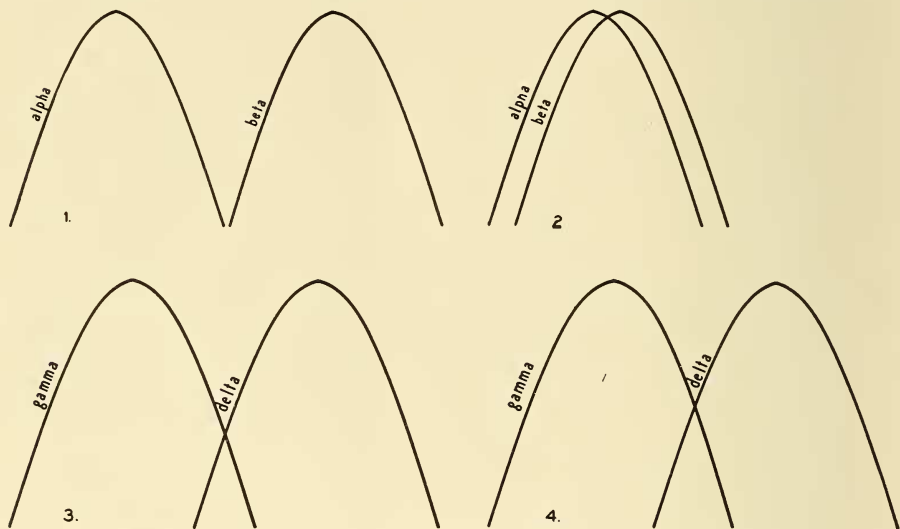


Fig. 1.—Graphic representation of frequency distributions of character *A* in two hypothetical populations, *alpha* and *beta*. Fig. 2.—Graphic representation of frequency distributions of character *B* in two hypothetical populations, *alpha* and *beta*. Fig. 3.—Graphic representation of frequency distributions of character *C* in two hypothetical populations, *gamma* and *delta*. Fig. 4.—Graphic representation of frequency distributions of character *D* in two hypothetical populations, *gamma* and *delta*.

as compared with that between the second pair, may be indicated by some measure expressing the extent of divergence of the principal character in the two pairs, characters *A* and *C*, respectively. But how are we going to combine the divergence of the two characters in each pair of populations in order to compare the relative divergence of the two pairs? Apparently a combination that will include the full measure of divergence of each character separately will likely show a higher relative divergence of the second pair of populations, a misleading result. If we are to include the lesser diverging character in the measure of divergence, it must be weighted, and weighted so that it will have only a very minor effect on the measure as determined by the

single character showing the greatest divergence. The development of a satisfactory method of weighting to produce a pertinent index of divergence is problematical. It seems apparent that a measure of divergence based only on the character showing the greatest divergence is fairly adequate, although perhaps not altogether complete, as an expression of the relative divergence of the above two hypothetical pairs of populations.

It should not be difficult to find in nature examples approximately corresponding to the above hypothetical cases. The same order of reasoning may be applied to three or more characters, and to the untold multitude of actual cases that may be encountered in practice.

Measures that have been proposed based on a combination of several characters are unsatisfactory. A few examples of such measures are next cited and discussed.<sup>2</sup>

Physical anthropologists have been using such a measure, designated as the "coefficient of racial likeness." This was devised chiefly for use in cases in which only small samples are available, on the assumption that the study of many characters and the combination of the sum of their differences in a single figure will compensate for the paucity of individuals studied and yield comparative figures that would be more reliable than those based on the comparison of a single character (see Pearson, 1926). Of course, the same measure may be applied to samples of fair or large size. The formula in use for determining this measure depends chiefly on the following factors: (1) the difference between the means of any one character of the two populations compared, (2) the standard deviation, (3) the number of specimens in the samples, (4) the summation of the values for the separate characters, (5) division of the value obtained by the number of characters. When a sample is small the standard deviation determined by it is unreliable, and that of the nearest related population for which an adequate sample is available is employed on the assumption that anthropometric data usually have a nearly normal distribution and that there is not much difference between the standard deviations of the different populations.

Seltzer (1937) discusses some of the errors and fallacies inherent in the "coefficient of racial likeness" when used as a measure of di-

<sup>2</sup> Students of the differing frequency distributions of blood groups in different populations of the genus *Homo* have been using a "biochemical index" or other indices to express population differences in terms of a single figure. These indices do not represent a combination of two or more characters, but a combination of percentage ratios of frequencies in the same distribution. As may well have been expected, such indices as well are inapplicable and sometimes misleading (see Wiener, 1935, pp. 153-154).



vergence, as follows: (1) For any given character, it assumes arbitrarily and unjustifiably a single standard deviation for different populations. (This objection may be overcome when the samples compared are of fair size, and the standard deviation of each population separately determined.) (2) It depends on the number of characters used in the comparison. (3) It depends on the number of specimens in the samples. (4) Fundamentally, it is not a measure of divergence, but rather an expression of probability. (5) What is most important of all, Seltzer shows that biologically it is altogether inapplicable, because it results in absurdly misleading conclusions. (The last three objections I raised in my 1938 paper in connection with the application of current formulae to a single character for the purpose of measuring divergence. The very fact that the coefficient of racial likeness is an expression of probability should lead one to expect that it will often result in false conclusions when used as a measure of divergence.)

Much simpler methods of combining several characters have been employed by some students of fishes in comparing populations or samples. Hubbs and Whitlock (1928, p. 471) compare two samples by determining the value of a ratio the numerator and denominator of which represent the products of measurements of certain parts, respectively, of the head and body. Koelz (1929, p. 426) also uses a ratio to express, in part, the difference between two populations (designated by him as subspecies), but the numerator and denominator represent the sums of the numerical value of two measurements. Schultz and Welander (1934, p. 6) employ the simple addition of the number of anal, dorsal, and both pectoral rays to determine the difference between two species. Similarly, Hubbs and Kuhne (1937) employ the sum of the numbers of anal, dorsal, ventral, and pectoral rays and the scales to determine the difference between two populations (designated by them as subspecies). Schultz and Schaefer (1936, p. 5) go a step farther and compare certain populations by both the addition and subtraction of the numerical values of certain characters, and the same device is employed by Schultz and Thompson (1936, p. 74), by Schultz and Reid (1937), and by Schultz (1937, p. 19).

By any of the above devices of combining characters, the numerical value of the combination is determined for each individual separately. A frequency distribution may then be arranged based on the individual numbers thus obtained.



For the purpose of determining relative divergence, or the taxonomic rank of the particular pair of populations compared, the combination of characters as determined by the above workers is inapplicable because it will prove to be misleading in many cases. Its use as a measure of divergence is therefore excluded for this one reason, outside of any other consideration. It is readily conceivable that by the use of such figures in the form of frequency distributions, some races may be shown erroneously to diverge to a greater extent than some species. It should not be difficult to find examples in nature to prove the truth of this assertion.

Judged by the evidence presented in one of the papers cited above, that by Schultz (1937), the two populations compared, *Mallotus villosus* and *M. catervarius*, are evidently not more than races, or subspecies at the most. Schultz compares in detail a larger number of characters than usual in such cases. It is work done in a thorough manner by methods that will help us solve the species problem. It is unfortunate, therefore, that his frequency distribution tables were not published, so that we could judge the precise divergence of every character separately. However, judged by the summaries of his data presented, the ranges and the means, it seems evident that the two populations intergrade widely in every character. Yet, when a certain number of characters are combined, by addition and subtraction, a frequency distribution is obtained that even shows a gap between the two populations. It should be possible to obtain the same result with many pairs of races if they are studied in as great detail as Schultz studied the pair of populations mentioned.

Another important matter to consider in this connection is the number of diverging characters. Let us take, for instance, two populations, *epsilon* and *zeta*, whose divergence in one character is close to 100 percent, or, concomitantly, intergradation is close to zero; and suppose, furthermore, that they do not diverge very appreciably in any other character. Nearly every individual may thus be referred to either population by the single, widely diverging character, and the two populations are to be properly regarded as distinct species. Now, let us suppose two other populations, *eta* and *theta*, that differ by, say, ten diverging characters, and furthermore, that there is considerable intergradation in every character, so that divergence of any one character is not more than of racial magnitude. In that case the two populations are to be properly regarded as of racial rank only, yet if the numerical values of the several characters are combined by the methods employed by the above authors, the two populations may

show a high degree of divergence, perhaps even a gap between them, higher than the divergence between populations *epsilon* and *zeta*. The two populations studied by Schultz, mentioned above, apparently constitute an example very similar to our hypothetical *eta* and *theta*.

The foregoing discussion relates chiefly to the device of combining the numerical value of characters by addition and subtraction. The same misleading results will be obtained by combining characters in the form of ratios or by division. A consideration of this manner of combining characters may be simplified by reducing it to its lowest terms, the combination of two characters. In the two hypothetical pairs of populations illustrated above, for instance, let us assume that character *D* differs in such manner that it has a greater numerical value in population *gamma* than in *delta*, that is, the left-hand curve in Fig. 4 represents *delta* while the right-hand curve represents *gamma*. Then, if we combine the two characters in the form  $\frac{C}{D}$ , it seems apparent that, for most specimens at least, the values  $\frac{C}{D}$  will be relatively greater for *delta* than for *gamma*, than in the comparison of the values of *C* alone. (This will depend to some extent, in individual specimens, on the degree of correlation of the two characters in each one of the two populations; but in general, the above statement may be expected to hold.) Consequently, the two arbitrary frequency distributions obtained from the values  $\frac{C}{D}$ , representing *gamma* and *delta*, respectively, will evidently show a greater divergence than either *C* or *D* taken separately. On the other hand, if we suppose that the numerical value of the characters *A* and *B* remain as illustrated, then the arbitrary distributions obtained by the combination  $\frac{A}{B}$  will likely show a lesser degree of divergence than that shown by the divergence of character *A* when considered by itself. In other words, by combining the two characters in each pair of populations as indicated, *gamma* and *delta* may show a higher degree of divergence than *alpha* and *beta*, evidently a misleading result. When the numerator or denominator, or both, are, in their turn, made to represent a combination of more than one character, by addition, subtraction, or multiplication, things become more complicated, but it is apparent from the foregoing discussion that combining characters in such manner will often result in misleading conclusions.

Such combinations of characters by addition, subtraction, multiplication, and division of their numerical values, when carried to their extreme as is done in some of the papers cited above, on the whole give the impression of a mere manipulation of figures rather than that of sound statistical treatment of the data. This impression appears

justified by the misleading results that are apt to occur. Fundamentally, what taxonomists are actually doing in distinguishing species, subspecies, or races, either by a numerical combination of several characters or by a consideration of every character separately, is to determine the relative degree of divergence; although this idea is often lost sight of on superficial thought. Our basis of comparison is, of course, always a single pair of populations. We determine to what degree a pair under consideration diverges and compare this divergence in relation to divergences shown by other pairs, either in a definite manner as I (1938) have suggested, or by rule of thumb as is usually done in taxonomic practice. That is just what most of the above-mentioned authors set out to accomplish, to determine by combining several characters the relative divergence of their populations, for the purpose of deciding whether they represent distinct species or categories of lower rank. For this purpose, their device of combining several characters is altogether misleading. What is particularly misleading in the use of such devices is that the 'arbitrary frequency distribution obtained as a result of the combination of the several characters may be treated by the ordinary statistical methods—as, indeed, a wholly mythical frequency distribution may be treated—to determine the value of the standard deviation, the probable error, the probability ratio, etc. Such treatment, seemingly, covers the figures with a cloak of statistical respectability, so to speak; it gives them a seeming validity. But, biologically, for the purpose of determining relative divergence, the figures are misleading, as discussed.

The foregoing devices of combining characters, in their extreme form, are carried to a point where they constitute almost a *reductio ad absurdum* going to prove their inapplicability. One is then compelled to reexamine the entire question more fully and work backward to the more simple forms. As a consequence, the applicability of some proper appearing, simple methods of combining characters is cast in doubt. For instance, it is the general impression among taxonomists that it is proper to use a ratio of two given measurements for the purpose of distinguishing species or populations of lower rank. I have used this method for distinguishing *Gobiosoma bosci* from *G. robustum* in my revision of their genus, and I used (1938) that comparison as one of the examples in establishing a gradual series of relative divergences. I (1929, p. 80) have also used the same method, in part, in comparing two populations of *Cynoscion*. Other taxonomists, and physical anthropologists in particular, sometimes

use character indices in the form of a ratio based on the numerical value of two measurements. Doubt is now cast on the propriety of treating the data in this manner for the purpose of determining relative divergence.

From this point of view, one of the general, basic methods of fish taxonomy needs a reappraisal. Measurements of various parts are generally used in distinguishing populations of fishes of specific or lower rank. The measurements are generally stated not as absolute values, but as the numerical value of a ratio, generally as entering so many times in the standard length (that is the combined length of head and body), or in the head. Sometimes a ratio is stated in percentage form. This method is adopted because measurements differ with the size of the individual, and consequently absolute measurements would often be of limited value unless they were based on individuals of approximately the same size. At any rate, measurements as generally employed in distinguishing populations of fishes are used as a combination of two characters. In view of the foregoing discussion, it may be asked, Do they form a legitimate basis for the determination of relative divergence?

It is well to emphasize here the distinction between two ideas or processes, namely, identification and determination of relative divergence. A combination of the numerical values of two or more characters to form an index may be useful in identifying specimens. However, identification is not the only function of taxonomy. By a comparative study of morphology taxonomists are also trying to interpret relationship. And what is of greater immediate importance, they are classifying populations into categories—species, subspecies, races, etc. For the latter purposes we need to determine relative divergence as precisely as possible, and for this determination the combination of the numerical values of several characters will often prove misleading. These values may be shuffled so that a pair of races may show a greater degree of divergence than a pair of species, and a pair of closely related species a lesser degree of divergence than a pair of races compared. It remains to be determined to what extent and how often the combination of two characters in the form of a ratio, such as the cephalic index of physical anthropologists, or the manner of expressing measurements employed by fish taxonomists, may be used in expressing relative divergence and how often it will be misleading for this purpose.

It has been stated above that for the purpose of a precise determination of relative divergence, the principal character constitutes a



basis for an adequate measure with respect to time and fairly adequate with respect to extent. Not only that, but the foregoing discussion makes it evident that it is the only proper basis now available. It is doubtful whether the other characters are to be considered at all in determining the measure of divergence, and in any case they should be afforded a very minor weight. The proper basis of determining such weights is not apparent now. In determining relative divergence every character must be considered separately, and apparently the best we can do now is to consider the other characters in a general way, in pairs of populations standing near the border line between the species and the subspecies, or the subspecies and the race, as determined by the principal character, as was suggested in my 1938 paper. The proper consideration of the other characters in this manner will, of course, depend on the thoroughness, skill, insight, and intuitive capacity of the taxonomist.

Other difficulties in the way of combining several characters appear altogether insurmountable. One of these is the possible existence of unequal numbers of diverging characters as between two or more given pairs of populations. This point has been raised above and hypothetical examples cited. Let us suppose further that one pair diverges in ten and another in twenty characters. Apparently, by combining all the characters in both cases, the two measures thus obtained will not express fairly the relative divergence of those two pairs of populations. To limit ourselves to a certain definite and equal number of characters in both pairs, as is done by Morant (1928), for instance, is a wholly arbitrary procedure; because on the assumption that the other characters, besides the principal one, are of importance in determining the measure of divergence, they should all be included in a determination of that measure for any one given pair of populations.

Another insurmountable difficulty is that it is practically impossible to study all characters. This is especially true if we are to include measurements of the head, body, or separate organs, or parts of the head, body, or organs, or the distance between any two given points, measurements by which distinct populations usually differ more or less. The number of such characters may be almost indefinitely increased. In practice, therefore, the number of characters studied necessarily must be limited, and the determination of divergence somewhat incomplete as far as it relates to the minor characters.

From the foregoing discussion the conclusion is reached that the principal character forms a fairly adequate basis for a measure of

divergence of a given pair of populations, which may be used in determining relative divergence in a series of pairs. It is the only appropriate basis now available. The other characters, if considered at all for this purpose, should be given very minor weights. In any case, it is practically impossible to include all the minor characters.

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